THE MESOPSYCHIDAE (MECOPTERA) OF THE QUEENSLAND TRIASSIC

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Abstract

The Mesopsychidae is an extinct family of Mecoptera now known to possess long siphonate mouthparts. Two species of mesopsychids are recorded from the Queensland Triassic: Mesopsyche triareolata Tillyard from the Late Triassic Blackstone Formation at Denmark Hill and Dinmore and Mesoses gayndah sp. n. from the early Middle Triassic Gayndah Formation at Gavndah. Mesopsyche triareolata is important as the type species of the type genus of Mesopsychidae but our knowledge of its venation still relies on Tillyard's now out-dated original descriptions and illustrations. Based on a re-examination of all Denmark Hill type and previously recorded specimens, as well as newly collected material from Dinmore, a full description and new illustrations of its venation are provided in order to inform any future revision of Mesopsyche Tillyard, which now includes a diverse assemblage of 10 species from the Permian and Triassic. Mesoses gayndah sp. n., known only from the holotype forewing, is a much larger species that is very similar to the South African Late Triassic Mesoses magna Riek. A preliminary diagnosis (based on the forewing only) of Mesoses Riek notes its similarity to Mesopsyche, especially in sharing the distally placed, long, backwardly curved base of CuA, but differentiates it on the absence of costal crossveins, the longer and much more deeply forked Sc, the posteriorly curved branches of Rs and the more distal forking of MA relative to Rs.

Introduction

In the first of his classic papers on the Mesozoic insects of Oueensland, Tillyard (1917) established the family Mesopsychidae for two species, Mesopsyche triareolata Tillyard and Triassopsyche dunstani Tillyard, based on wing fragments from the Triassic Blackstone Formation at Denmark Hill. southeastern Oueensland. As implied by the 'psyche' root of the generic names. Tillvard contended that the species were the oldest Trichoptera. When he later added two more Denmark Hill wing fragments to the family, Aristopsyche superba Tillyard and Neuropsyche elongata Tillyard, Tillyard (1919) revised his opinion and established a new order Paratrichoptera, noting, however, that the presence of a simple CuA in all four species was 'of a type seen in all fossil and recent Mecoptera' (Tillyard 1919, p. 205). In his re-examination of the mecopteroid insects from Denmark Hill, Riek (1956) confirmed the Mesopsychidae as Mecoptera, determined that Tillyard's four species were indeed conspecific (as M. triareolata) and correctly identified the types of M. triareolata and N. elongata as hindwings and those of T. dunstani and A. superba as forewings.

Since that time, the Mesopsychidae has been considerably augmented with the addition of 10 genera from the early Permian to early Cretaceous of Australia, China, Kyrgyzstan, Russia, South Africa, Tajikistan and Ukraine (Shih *et al.* 2013). On the basis of wonderfully preserved Chinese mesopsychid specimens, it is now also known that species of the family had 'elongate, siphonate (tubular) proboscides and fed on ovular secretions of

extinct gynmosperms' (Ren et al. 2009, p. 840). The cladistic analysis performed by Ren et al. (2009) proposed that the Mesopsychidae and the Aneuretopsychidae other siphonate mecopteran families. and Pseudopolycentropodidae, form the monophyletic group Aneuretopsychina, which they considered to be the sister taxon of the remaining Mecoptera. Bashkuev (2011a) further augmented the Aneuretopsychina with the addition of a new family of Permian and Triassic long-proboscid scorpionflies, the Nedubroviidae. More recently, however, Bashkuev (in litt.) has proposed, on grounds of mouthpart morphology and venation, that the the Aneuretopsychina comprise only the Mesopsychidae and Aneuretopsychidae, whereas the Pseudopolycentropodidae and Nedubroviidae are members of a separate monophyletic siphonate mouthpart group.

Notwithstanding the substantial increase in knowledge of the diversity and biology of the Mesopsychidae, the taxonomy of its type genus, *Mesopsyche* Tillyard, remains unsatisfactory. As a result of the works of Novokshonov (1997), Novokshonov and Sukacheva (2001) and Bashkuev (2011b), it now includes a diverse assemblage of 10 species from the Permian and Triassic and requires a comprehensive revision (Bashkuev 2011b). Even though Bashkuev (2011b), at the suggestion of Novokshonov and Sukacheva (2001), synonymised the South African *Mesoses* Riek with *Mesopsyche*, taking into account the present knowledge of the taxonomy of *Mesopsyche*, I agree with Shih *et al.* (2013) and prefer to retain Riek's genus as distinct. Its two species are therefore not included in the 10 mentioned above.

Through the efforts of Andrew Rozefelds of the Queensland Museum and local fossil collectors Allan Carsburg and Robert Knezour, there are now three new forewing and three new hindwing specimens of *M. triareolata*, the type species of *Mesopsyche*, all collected from the Blackstone Formation at Dinmore, southeastern Queensland. One of the hindwings is particularly impressive, being almost complete and preserving the all-important wing base. To assist any future revision of *Mesopsyche*, the purpose of the present work is to give a full account of the venation of *M. triareolata*, based on an examination of all available material, *viz*. Tillyard's four Denmark Hill types, the Denmark Hill hindwing mentioned by Riek (1956) and the six new specimens from Dinmore. Additionally, the opportunity is taken to record a second Queensland mesopsychid, a new species from the Middle Triassic Gayndah Formation, which is of a size and venation very similar to those of the South African Late Triassic *Mesoses magna* Riek.

The venational nomenclature follows that of Bashkuev (2011b), although for the sake of clarity I have named the crossveins quite precisely, *i.e.* after the specific longitudinal veins they join. The line drawings were prepared using a camera lucida attachment on a Motic stereomicroscope. To facilitate comparison, all specimens are figured as right wings. Abbreviations for collections are as follows: ACC – Allan Carsburg Collection, Brisbane (to be deposited in QM); AM – Australian Museum; GSQ – Geological Survey of Queensland (all specimens transferred to QM); QM – Queensland Museum; UQ – University of Queensland (all specimens transferred to QM).

The fossil localities

The Denmark Hill *Mesopsyche* recorded by Tillyard and Riek were collected in grey shales of the Late Triassic (Carnian) Blackstone Formation, the uppermost member of the Ipswich Coal Measures (Purdy and Cranfield 2013). The exposure, which is no longer accessible, was in a small quarry in what is now the Denmark Hill Conservation Park (-27.622° 152.756°) in the city of Ipswich. The site was documented in detail by Dunstan (1923).

The Dinmore locality (-27.606° 152.827°), also in the Blackstone Formation, is a small commercial clay pit in Dinmore, a suburb of Ipswich, approximately seven kilometres east of Denmark Hill. The site has been well documented by Rozefelds and Sobbe (1987). The lithology and composition of the insect fauna are more or less identical to those of Denmark Hill.

The Gayndah species recorded herein was collected in shales of the early (Anisian) Middle Triassic Gayndah Formation (Purdy 2013) in a road cutting (-25.615° 151.640°) approximately three kilometres ENE of the town of Gayndah. Two species of Neuroptera have also been recorded from the same site (Lambkin 1988, 2014).

Family Mesopsychidae Tillyard

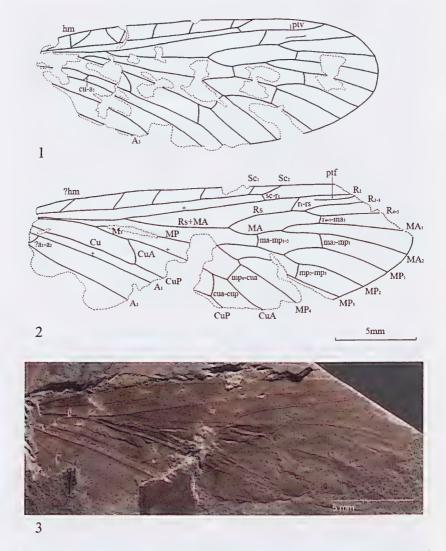
Mesopsyche triareolata Tillyard

(Figs 1-13)

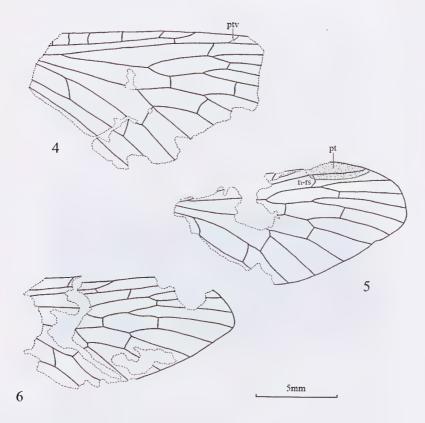
Mesopsyche triareolata Tillyard, 1917: 182, text-fig. 2, plate vii, fig. 1. Triassopsyche dunstani Tillyard, 1917: 184, text-fig. 3, plate vii, fig. 2. Aristopsyche superba Tillyard, 1919: 202-203, text-fig. 25. Neuropsyche elongata Tillyard, 1919: 204-205, text-fig. 26.

Material examined. Holotype of *M. triareolata* AM F.39233 ('Pres[ented by]. Mrs R.J. Tillyard 1940'), Denmark Hill, incomplete right hindwing, part only, length 12.5 mm, width 5.5 mm; *holotype* of *T. dunstani* AM F.39228 ('Pres. Mrs R.J. Tillyard 1940'), Denmark Hill, incomplete right forewing, part only, length 13.5 mm, width 7 mm; *holotype* of *A. superba* AM F.39263 ('Pres. Mrs R.J. Tillyard 1940'), Denmark Hill, almost complete left forewing, part only, length 21.5 mm, width 8 mm; *holotype* of *N. elongata* AM F.39272 ('Pres. Mrs R.J. Tillyard 1940'), Denmark Hill, incomplete left forewing, part only, length 12 mm, width 5.5 mm; UQ C.2046-2047 (Riek 1956, fig. 1), Denmark Hill, incomplete right hindwing, part and counterpart, length 18 mm, width 7 mm; QM F.57541, Dinmore, almost complete right forewing, part and counterpart, length 13 mm, width 7.5 mm, collected by R. Knezour; QM F.57543, Dinmore, incomplete left forewing, part and counterpart, length 15 mm, width 9 mm, collected by R. Knezour; ACC I.27, Dinmore, almost complete left hindwing, part and counterpart, length 15 mm, width 9 mm, collected by R. Knezour; ACC I.27, Dinmore, almost complete left hindwing, part and counterpart, length 12 mm, width 12.5 mm, collected by R. Knezour; ACC I.27, Dinmore, almost complete left hindwing, part and counterpart, length 19 mm, width 12.5 mm, collected by R. Knezour; ACC I.27, Dinmore, almost complete left hindwing, part and counterpart, length 19 mm, width 12.5 mm, collected by R. Knezour; ACC I.27, Dinmore, almost complete left hindwing, part and counterpart, length 19 mm, width 12.5 mm, collected by R. Knezour; ACC I.27, Dinmore, almost complete left hindwing, part and counterpart, length 19 mm, width 12.5 mm, collected by R. Knezour; ACC I.27, Dinmore, almost complete left hindwing, part and counterpart, length 19 mm, width 12.5 mm, collected by R. Knezour; ACC I.27, Dinmore, almost complete left hindwing, part and counterpart, length 19 mm, width 12.5 mm, collected by R. Knezour; ACC I.27, Dinmore, a

by A. Carsburg; QM F.14009, Dinmore, incomplete right hindwing, part and counterpart, length 21 mm, width 8.5 mm, collected by A. Rozefelds, October 1985; QM F.14301a,b, Dinmore, incomplete left hindwing, part and counterpart, length 12 mm, width 7 mm, collected by A. Rozefelds, March 1986.

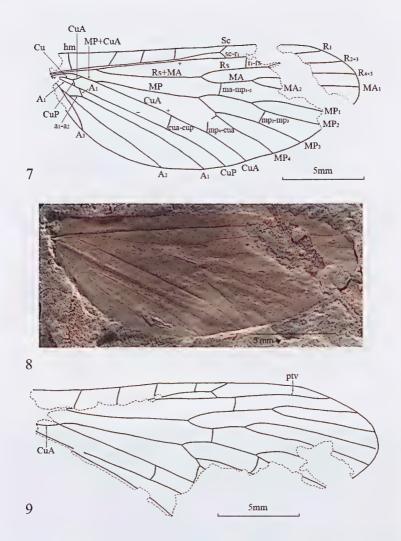


Figs 1-3. *Mesopsyche triareolata* forewings: (1) AM F.39263, holotype of *Aristopsyche superba*, Denmark Hill; (2-3) QM F.57541, Dinmore. *hm* humeral vein; *ptf* pterostigmal furrow; *ptv* pterostigmal veinlet.



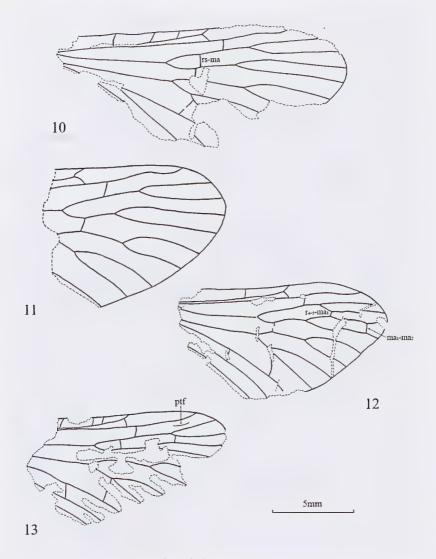
Figs 4-6. Mesopsyche triareolata forewings: (4) QM F.57543, Dinmore; (5) QM F.57542, Dinmore; (6) AM F.39228, holotype of Triassopsyche dunstani, Denmark Hill. pt pterostigma; ptv pterostigmal veinlet.

Description. Forewing (Figs 1-6). Size and shape apparently somewhat variable, larger specimens with estimated length 23-25 mm, width c. 8 mm, apex rounded (Figs 1-4), smaller specimens width c. 7 mm, apex more acute (Figs 5-6). QM F.57541 with an indication of a colour pattern, the membrane noticeably darker anteriorly and along several longitudinal veins and crossveins, for example the base of CuA and cua - cup (Fig. 3). Costal margin slightly convex. Costal space narrowed apically, with at least 4 crossveins (including humeral vein) somewhat variable in shape and inclination, probable humeral vein of QM F.57541 notably inclined (Fig. 2) in contrast to that of the holotype of A. superba, which is upright and noticeably thickened over its basal half (Fig. 1); holotype of A. superba with additional (apparently aberrant) costal crossveins, a curved one originating from base of humeral



Figs 7-9. Mesopsyche triareolata hindwings: (7-8) ACC I.27, Dinmore; (9) QM F.14009, Dinmore. hm humeral vein; ptv pterostigmal veinlet.

vein, a second backwardly inclined one from Sc just proximal to the base of the second upright crossvein, and possibly a third (preservation not clear) strongly inclined one at the extreme base of the wing (Fig. 1). Sc terminating on costal margin at about ³/₄ wing length, with a short apical fork, well



Figs 10-13. *Mesopsyche triareolata* hindwings: (10) UQ C.2046-2047, Denmark Hill; (11) QM F.14301a, b, Dinmore; (12) AM F.39233, holotype of *M. triareolata*, Denmark Hill; (13) AM F.39272, holotype of *Neuropsyche elongata*, Denmark Hill. *ptf* pterostigmal furrow.

beyond the Rs - MA fork. R_1 convex, quite widely separated from Sc, curved posteriad at pterostigma, two specimens with very weak and incomplete single pterostigmal veinlets (Figs 1, 4). Pterostigmal furrow at least indicated

in most specimens, pterostigma most clearly defined in OM F.57542 as a slightly darker and more crinkled area of the wing membrane (Fig. 5). Rs -MA fork quite broad, Rs and MA each with 2 guite long branches, branches of Rs more or less straight, not curved posteriad. MA fork proximal to that of Rs. Neither nodal line nor thyridulum or thyridium detected. MP with 4 branches, quite widely spaced compared with those of Rs and MA, MP₃₊₄ fork proximal to that of MP_{1+2} . CuA convex, its base strongly backwardly inclined and in most specimens notably sigmoidal, forming an obtuse cubitomedial Y-vein with a long M₅. CuP not noticeably convex or concave. Intercubital space and space between M and Cu guite broad. Anal veins, as far as preserved, long and parallel, A₁ convex. Crossveins consistent in position and number: a short, backwardly inclined apical sc - r_1 ; a forwardly inclined, slightly sigmoidal r_1 - rs just beyond the apex of Sc (the kink in this crossvein in QM F.57542 (Fig. 5) is a preservation artefact); a short r_{4+5} - ma₁ just beyond the Rs fork; a straight or curved ma - mp_{1+2} ; a straight or slightly curved ma₂ - mp₁; a straight or slightly curved mp₂ - mp₃; a straight or slightly curved mp₄ - cua (in QM F.57543 (Fig. 4) arising at the MP₃₊₄ fork); a backwardly inclined, curved cua - cup, in some specimens somewhat paralleling the curvature of the base of CuA; a short, forwardly inclined cu a_1 (but only detected in holotype of A. superba – Fig. 1); a possible basal, sigmoidal $a_1 - a_2$ (uncertain preservation in QM F.57541 – Fig. 2).

Hindwing (Figs 7-13). Size and shape apparently somewhat variable, larger specimens with estimated length 19-22 mm, width 7.5-9 mm, apex rounded (Figs 7-11), smaller specimens width c. 6 mm, apex more acute (Figs 12-13). Costal margin straight. Costal space narrowed apically, with at least 4 crossveins (including humeral vein) slightly variable in shape and inclination, humeral vein slightly backwardly inclined and noticeably thickened over its basal half (Fig. 7). Sc simple, terminating on costal margin just beyond $\frac{1}{2}$ wing length, running closely parallel to R_1 for $\frac{3}{4}$ length, then curved anteriad, apex forming a Y with sc - r_1 ; R_1 convex, curved posteriad at pterostigma, one specimen with the suggestion of a pterostigmal veinlet (Fig. 9). Pterostigmal furrow preserved in one specimen (Fig. 13). Rs - MA fork slightly narrower than in forewing, Rs and MA each with 2 quite long branches, MA fork proximal to that of Rs. Neither nodal line nor thyridulum or thyridium detected. MP with 4 branches, only slightly more widely spaced than those of Rs and MA, MP_{3+4} fork proximal to that of MP_{1+2} . Base of Cu preserved as a Y-vein as in recent Mecoptera, the CuP arm of the Y a weaker vein than the CuA arm. In the two specimens where preserved, the point of fusion of CuA and MP variable, much more basal in ACC I.27 (Fig. 7) than in the larger QM F.14009 (Fig. 9). Main section of CuA convex. CuP concave, fused with A1 for a short length. CuA, CuP, A1 and A2 long and more or less parallel, fairly evenly spaced. The base of A₁ after its separation from CuP oblique, forming one arm of a Y vein with the equally oblique a_1 a_2 . A_2 and A_3 fused basally, strongly divergent apically. Crossveins generally

consistently less clearly preserved than in forewing, those which appear to be present as follows: a backwardly inclined apical sc - r_1 , noticeably longer than in forewing; a more or less upright, slightly curved r_1 - rs just beyond the apex of Sc; a very slightly curved ma - mp_{1+2} ; a long mp_4 - cua (from MP₃₊₄ in holotype of *N. elongata* – Fig. 11) which may be straight, angular, curved or sigmoidal, and often appearing incomplete at about ½ length; a straight or curved cua - cup at about CuA ½ length; an oblique $a_1 - a_2$. Other less consistently present (or less preserved?) crossveins: an upright rs - ma just beyond the Rs - MA fork detected in 2 specimens (Figs 10, 13); a short r_{4+5} ma₁ just beyond the Rs fork detected in two specimens (Figs 12, 13) and suggested by a kink in Rs₄₊₅ in a third specimen (Fig. 10); a distal ma₁ - ma₂ detected in one specimen (Fig. 12); a straight or curved mp_2 - mp_3 detected in 2 specimens (Figs 7, 9).

Notes. Even though there is some variation in wing size and shape, this is considered as no more than intraspecific variation. A similar magnitude of size variation has been recorded in the Russian Upper Permain mesopsychid *Permopsyche issadensis* Bashkuev, albeit a much smaller species (Bashkuev 2011b). It has also been found (Shih *et al.* 2013) that mesopsychids demonstrate size and wing shape asymmetry for the left and right wings of individual specimens. This phenomenon may also account for some of the variation recorded for *M. triareolata.* The above description is consistent with the most recent diagnosis of the genus *Mesopsyche* (Bashkuev 2011b), acknowledging the misprint of CuP instead of CuA in the text of his diagnosis (Bashkuev pers. comm.).

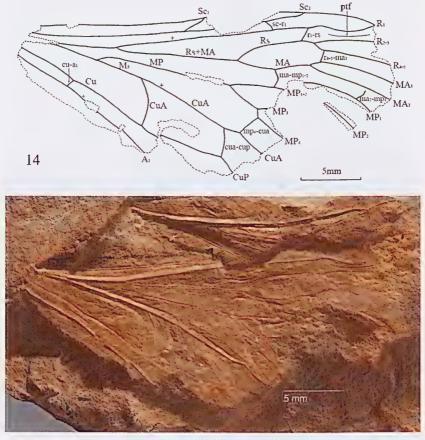
Genus Mesoses Riek

Mesoses Riek, 1976: 816. Type species M. optata Riek (original designation).

Diagnosis. Forewing similar to that of *Mesopsyche triareolata*, but with the following differences: Costal space without crossveins, not tapered apically; Sc terminating on costal margin beyond $\frac{3}{4}$ wing length, forked early, just beyond $\frac{1}{2}$ length, well basal of Rs - MA fork; R₁ strongly curved posteriad at pterostigma; branches of Rs curved posteriad (see Schlüter 1997, figs 5a, 5d); MA fork at about the same level as that of Rs, or slightly more distal.

Notes. Riek's original generic diagnosis was based on his placement of *Mesoses* in a new family, Mesosetidae, of Lepidoptera, and thus he did not distinguish it from *Mesopsyche*, the type genus of the Mesopsychidae. The only distinguishing character alluded to by Riek and subsequently referred to by Novokshonov (1997) was the lack of costal crossveins. As the above diagnosis indicates, *Mesoses* and the type species of *Mesopsyche* are very similar, most especially in sharing the very characteristic (and presumably apomorphic) long, backwardly curved base of CuA, which forms an obtuse cubito-medial Y-vein with a long M_5 . As it is based only on a comparison of the specimens of *Mesoses* described by Riek (1976), Schlüter (1997) and

herein, with the type species of *Mesopsyche*, the above diagnosis is therefore preliminary only, pending a full revision of mesopsychid generic relationships.



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Figs 14-15. Mesoses gayndah, holotype (forewing) QM F.57544, Gayndah. ptf pterostigmal furrow.

Mesoses gayndah sp. n.

(Figs 14-15)

Type and only specimen. Holotype, QM F.57544, Gayndah fossil insect locality, almost complete right forewing and fragmentary left forewing, part only, length of right forewing 29 mm, width 13 mm, collected by K.J. Lambkin, 1975.

Description. Forewing (Figs 14-15). Broad, length estimated at c. 35 mm, width at least 14 mm. Costal margin straight. Costal space narrow. R_1 convex, quite widely separated from Sc. Pterostigmal furrow deep. Neither nodal line nor thyridulum or thyridium detected. Base of MP, M₅ and longitudinal section of CuA convex. Cu \rightarrow CuP not noticeably convex or concave. Inter-cubital space and space between M and Cu very broad. A_1 long, parallel to Cu, convex. Crossveins: a short, backwardly curved apical sc - r_1 ; a forwardly inclined straight r_{4+5} - ma₁ just beyond the Rs fork; a strongly curved ma - mp₁₊₂; a strongly curved ma₂ - mp₁; a slightly curved mp₄ - cua; a backwardly curved cua - cup, but much less curved than the base of CuA; a short, straight, slightly forwardly inclined cu - a_1 .

Etymology. Named after the type locality.

Formation and Age. Gayndah Formation, early (Anisian) Middle Triassic.

Notes. Mesoses gayndah is very similar in size and venation to the South African Late Triassic M. magna Riek, which was based on a similar specimen, measuring 30 mm, and preserving about the same area of the forewing (Riek 1976, fig. 17). Mesoses gayndah differs from M. magna in the apparently straighter costal margin and narrower costal space and the presence of the following crossveins (all apparently absent in M. magna): $ma_2 - mp_1$, $mp_4 - cua$, cua - cup and cu - a_1 . It is conceded that the differences are quite trivial and that many, if not all of these crossveins are simply not preserved in the holotype specimen of M. magna. In this regard, it is of note that one of the unidentified Mesoses forewings figured by Schlüter (1997, fig. 5a), which on size and venation appears to be a more complete specimen of M. magna, does indeed possess all these crossveins with the exception of ma2 - mp1. On balance, however, notwithstanding its similarity to M. magna, for the sake of the record I believe that it is the better option to consider this older (Middle Triassic) and quite geographically distant Australian specimen as a distinct species.

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